A SYSTEMATIC STUDY OF *SILENE SUKSDORFII*, S. GRAYI, AND S. SARGENTII (CARYOPHYLLACEAE)

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Abstract

The taxonomic and geographic limits of *Silene suksdorfii*, *S. grayi*, and *S. sargentii* are not well defined in California. Specimens of *Silene* from subalpine and alpine regions have been regarded traditionally as either *S. grayi* or *S. sargentii*. Several collections from northern California possess features characteristic of *S. suksdorfii*. Evidence from morphological, ecogeographical, and phytochemical examinations is presented that clarifies the taxonomic relationships, delimits the differences among these species, and corroborates the existence of *S. suksdorfii* n California.

Silene has been the subject of several regional and worldwide taxonomic revisions (Williams 1896, Robinson 1897, Hitchcock and Maguire 1947, Chowdhuri 1957). Although many species are circumscribed clearly, others are polymorphic or possess characters that do not permit clear distinctions to be made, and information about the distribution and habitat(s) of these species often is lacking or defined poorly. Historically, subalpine and alpine specimens of *Silene* from the southern Cascade Range of California have been considered to be either *S. grayi* Wats. or *S. sargentii* Wats. The occurrence of *S. suksdorfii* Robins. on Mount Shasta has been overlooked generally, and examination of herbarium records and pertinent literature indicates that the distributional ranges of these three species are not well understood.

Robinson (1891), Hitchcock and Maguire (1947), and Chowdhuri (1957) commented on the similar morphology of *S. suksdorfii*, *S. grayi*, and *S. sargentii*. Traits that typically distinguish *S. suksdorfii* from *S. grayi* and *S. sargentii* are its shorter stature, shorter basal leaves, bilobed petal blades, and trichomes of the calyx that possess purple septal walls. *Silene suksdorfii* is differentiated further from *S. grayi* by the presence of anastomosing calyx veins, and from *S. sargentii* by epapillose seeds.

Hybridization studies by Kruckeberg (1955, 1961) showed that S. suskdorfii, S. grayi, and S. sargentii are distinct species. Kruckeberg (1955) ascribed the high degree of sterility in hybrids to meiotic abnormalities during microspore formation and observed little chromosome pairing in hybrids. Kruckeberg (1961) concluded that vegetative and reproductive features showed that extensive genetic dif-

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Table 1.	POPULATION 1	Designations	USED IN FIG	s. 1–4. * = pı	itative populations
of Silene gro	ayi and/or S. s	argentii deteri	nined to be	S. suksdorfii.	

	Silene suksdorfii				
BT	Broken Top, Three Sisters Wilderness Area, OR				
SS	South Sister, Three Sisters Wilderness Area, OR				
BU*	Bumpass Mt., Lassen Volcanic National Park, CA				
CRE*	Crescent Crater, Lassen Volcanic National Park, CA				
LA*	Lassen Peak, Lassen Volcanic National Park, CA				
SP*	South Plug, Lassen Volcanic National Park, CA				
RB*	Red Butte, Mount Shasta, CA				
	Silene grayi				
MM	Marble Mountain, Marble Mountains Wilderness Area, CA				
LMH	Little Mount Hoffman, Medicine Lake Highlands, CA				
PSM	Pumice Stone Mountain, Medicine Lake Highlands, CA				
PAN	Panther Creek Meadows, Mount Shasta, CA				
SHA	Glacial basin north of Red Butte, Mount Shasta, CA				
TAL	Talus at base of Red Butte, Mount Shasta, CA				

ferentiation in these and most other western North American *Silene* species was complete. In spite of their genetic isolation, these three species have similar morphology and ecological preferences, which have contributed to the confusion in their delimitation in California. The purpose of the present study is to examine these species by the use of morphological, ecogeographical, and phytochemical analyses to circumscribe them clearly.

MATERIALS AND METHODS

Specimens of *S. suksdorfii* and *S. grayi* were collected in Oregon and California (Table 1). Extensive collections of *S. sargentii* were not made during this study because the taxon is represented amply in California herbaria.

Field collections of *S. suksdorfii* and *S. grayi* were used in chemical analyses. Flavonoid compounds were extracted from dried flowers, purified, and identified using two-dimensional paper chromatography following standard techniques (Harborne 1967, Mabry et al. 1970). The first phase was developed in 4:1:5 butanol:glacial acetic acid:water (BAW); the second, in 15% glacial acetic acid. Rutin provided a reference marker. For spectrophotometric analyses, extracts from dried flowers were streaked onto Whatman 3 mm paper and developed in four solvent systems: BAW, 15% glacial acetic acid, BEW (4:1:2.2 butanol:ethanol:water), and water. Each band in each system was examined using UV light, with and without exposure to ammonia fumes. Identification of compounds was made using UV spectroscopy. Sugar moieties were not identified during

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	S. suksdorfii	S. sargentii	S. GRAYI
Stature ² , cm	3-10(-15)	10-15(-20)	10-20(-30)
Stem glandu- larity	glandular above; increases from base	glandular above	glandular above; can be eglandular below
Leaves ²	matted; linear to linear-oblanceo- late	tufted, marcescent; linear-oblanceo- late	tufted, thickened, ± fleshy; linear-ob- lanceolate to ob- lanceolate-spatu- late
Leaf glands	present	present	absent
Leaf length	(5–)15(–50)	15-25(-40)	(15-)20-40(-60)
Leaf width	1.5-2(-4)	(1-)1.5(-3)	(1-)2-5(-7)
Calyx length	10-14(-18)	(8-)10-14(-17)	(7-)10-12(-13)
Calyx trichomes ¹	purple-septate	hyaline-septate, rarely purple- septate	hyaline-septate
Calyx nerves ¹	anastomosing; purple	anastomosing; green-purple	nonanastomosing; green-purple
Petal claw	(7-)8-11(-13)	(8-)10-14(-17)	8-11
Petal blade	(3-)3.5(-5)	2.5-3.5(-5)	(3-)3.5(-5)
Petal lobing ²	bilobed with occa- sional small lat- eral teeth	bilobed with small lateral teeth	more or less four- lobed, rarely bi- lobed
Carpophore	(2-)2.5-3.5	1.5-3	(1.5–)2–3
Style number	3(4)	3(4.5)	3
Seed length ¹	$1.1-2.0$ ($\bar{x} = 1.6$)	$1.2-2.0$ ($\bar{x} = 1.5$)	$1.8-3.0$ ($\bar{x} = 2.3$)
Testa character ¹	tessellate	tessellate with marginal pa- pillae	tessellate

TABLE 2. MORPHOLOGICAL CHARACTERS AND DIAGNOSTIC FEATURES OF Silene suksdorfii, S. grayi, AND S. sargentii. Adapted in part from Hitchcock and Maguire (1947). 1 = definitive for species; 2 = variable, but definitive in combination with other characters. All measurements are in millimeters except where noted.

this study. Flavonoids isolated from putative populations of S. suksdorfii were compared to those extracted from different populations of S. grayi and S. suksdorfii. Flavonoids of S. sargentii were not examined because this species possessed distinctive morphological traits.

Morphological measurements were made using field and herbarium specimens to corroborate those given by Hitchcock and Maguire (1947). Statistical tests included F-test, Student's t-test, and arcsin transformation methods (Sokal and Rohlf 1973). Seeds were measured using a micrometer calibrated for use with a dissecting microscope.

Specimens were examined from CAS, DS, F, GH, JEPS, MO, NY, ORE, OSC, PH, UC, US, WS, and WTU. Voucher specimens are deposited in CAS, SFSU, and WTU. Nomenclature conforms to Munz (1959) and Hitchcock et al. (1969).

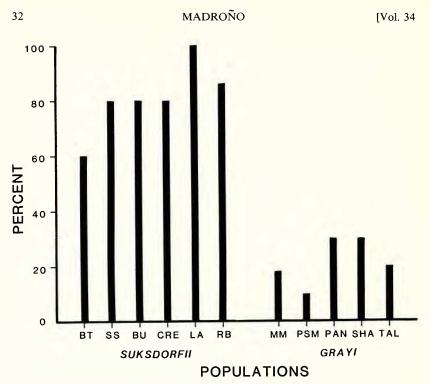


FIG. 1. Percent anastomosing calyx veins in populations of *Silene suksdorfii* and *S. grayi* (n = 40).

RESULTS

Morphology. Morphological characters were studied with specific reference to those given by Hitchcock and Maguire (1947) and are shown in Table 2. Traits that were valuable in the differentiation of *S. suksdorfii* from *S. grayi* and *S. sargentii* were the presence of purple-septate calyx trichomes, the absence of corolla lobes lateral to primary lobes, seed size, and lack of marginal papillae on seeds. Silene grayi and S. sargentii possess hyaline-septate calyx trichomes and corolla lobes lateral to primary lobes. Seeds of S. grayi are larger than those of S. sargentii or S. suksdorfii, and seeds of S. sargentii possess marginal papillae. Calyx venation is an additional feature by which S. suksdorfii and S. sargentii can be distinguished from S. grayi.

Robinson (1891) distinguished S. grayi and S. suksdorfii using calyx venation. He reported veins of S. grayi as simple and those of S. suksdorfii as anastomosing. An examination of specimens of S. sargentii also indicates that calyx veins are primarily anastomosing in this taxon. Although this trait is variable in these three species, presence or absence of anastomosing calyx veins can be a

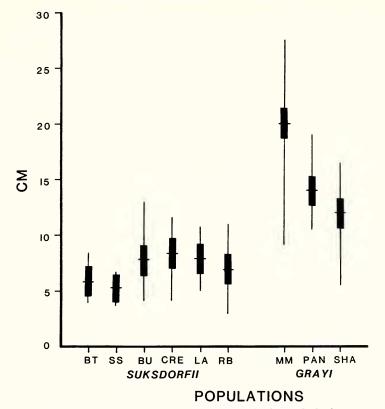


FIG. 2. Comparison of stem length in populations of *Silene suksdorfii* and *S. grayi* [n = 15; 1.96 \pm 1.3 ($\bar{x} \pm$ s.e.)].

significant feature. I found that the presence of anastomosing calyx veins in S. suksdorfii was significant in the differentiation of S. suksdorfii from S. gravi (p < 0.05). The differences between these species was greater than the natural variation within each species (Fig. 1). Anastomosing calvx veins in S. sargentii were not analyzed statistically due to inadequate sample sizes. Differences in calvx length/width between S. suskdorfii and S. gravi were not significant statistically (p > 0.05). In general, calvx size is not a reliable taxonomic trait in the differentiation of species of Silene because the developing capsule deforms the calyx, which renders field measurements inaccurate (Bocquet and Baehni 1961). Robinson (1891), Hitchcock and Maguire (1947) and Chowdhuri (1957) attributed shorter stature to S. suksdorfii than to S. gravi or S. sargentii. Leaves of S. suksdorfii were described similarly as being smaller than those of the other two species. In the examined populations, S. gravi is taller than S. suksdorfii (p < 0.05; Fig. 2). Stature in S. sargentii is

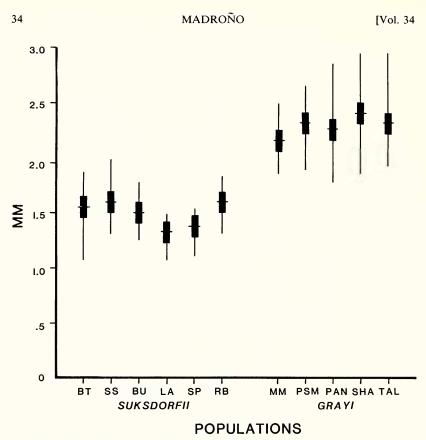


FIG. 3. Comparison of seed length in populations of *Silene suksdorfii* and *S. grayi* [n = 20; 1.96 \pm 0.09 ($\bar{x} \pm$ s.e.)].

similar to that of *S. grayi*. Differences in the size of basal leaves of *S. suksdorfii* and *S. grayi* were not significant (p > 0.05). The leaves of *S. suksdorfii* and *S. sargentii* appear narrower than those of *S. grayi*. Seed length in *S. suksdorfii* and *S. sargentii* was similar in range and average size. *Silene suksdorfii* had significantly different seed lengths in comparison to *S. grayi* (p < 0.05; Fig. 3).

Flavonoid analysis. The two-dimensional spot configuration was similar for S. suksdorfii and S. grayi, but iso-orientin, a c-glycosyl-flavonoid, was present on chromatograms of S. grayi.

Distribution. Silene suksdorfii occurs at elevations of 1800–3000 m, and is restricted to alpine environments on volcanic peaks in the Cascade Range. Prior to the present study, S. suksdorfii was reported solely from the major Cascade Range peaks of Oregon and Washington, and although Merriam (1899) reported correctly that S. suksdorfii occurred on Mount Shasta, its existence in California has been

48⁰

45⁰

420

.390

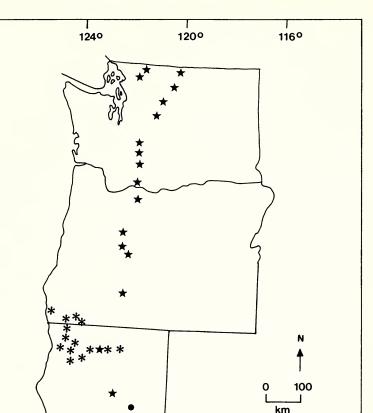


FIG. 4. Distribution of *Silene suksdorfii* (\bigstar), *S. grayi* (\ast), and *S. sargentii* (\bullet). Locations are based on herbarium specimens and from literature, and represent the corrected distribution of each species.

largely overlooked. In California, *S. suksdorfii* is represented by populations on Mount Shasta (Red Butte and Lake Helen) and on several peaks within Lassen Volcanic National Park (Table 1). *Silene grayi*, found at 1200–2900 m elevations, is an element of several disparate ecosystems: montane chaparral, montane forest, subalpine forest, and alpine. Substrates on which it occurs include gabbro, granite, marble, serpentine, andesite, and rhyolite pumice. It occurs

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in the Klamath Mountains Province of Oregon and California; in California, it also occurs in the Medicine Lake Highlands and on Mount Shasta, the type locality. *Silene grayi* is sympatric with *S. suksdorfii* on Mount Shasta. *Silene sargentii*, also an alpine species, occurs at elevations of 2400–3800 m, and is found primarily on granitic, metamorphic, and volcanic substrates. In California, it occurs on Sierra Nevada peaks from Inyo to Plumas cos.; in Nevada, it occurs on Mount Rose, and in the Monitor, Toiyabe, and Toquima ranges.

The distributions of S. suksdorfii, S. gravi, and S. sargentii reported previously in the literature are inaccurate due to misidentification of herbarium specimens. Collections reported as S. sargentii from the Cascade Range are either S. suksdorfii or S. parryi (Wats.) Hitch. & Maguire. Specimens identified as S. sargentii from the Klamath Mountains Province are collections of S. gravi. Similarly, individuals identified as S. gravi from the Cascade Range of Oregon and Washington are either S. suksdorfii or S. parrvi. The report of S. gravi from the Webber Lake Mountains, Sierra Co., California, by Hitchcock and Maguire (1947) is based on a collection of S. bernardina Wats. ssp. maguirei Bocquet (=S. montana Wats.). Collectors (Gillett et al. 1961) also have reported S. gravi from Lassen Volcanic National Park, California, but examination of specimens from this location revealed they are collections of S. suksdorfii. Several collections of S. douglasii Hook. from the Cascade Range and from Mount Olympus have been misidentified as S. suksdorfii. Some collections of S. sargentii also have misidentified as S. suksdorfii. The corrected distributional ranges for S. suksdorfii, S. gravi, and S. sargentii are illustrated in Fig. 4.

DISCUSSION

Morphology. There is considerable overlap of many morphological characters among S. suksdorfii, S. grayi, and S. sargentii, but seed size and morphology, calyx trichomes and venation, and petal lobing constitute a suite of taxonomic features useful in their differentiation.

The data presented here, in addition to the phylogenetic study of Williams (1896), offer several conclusions about the value of these morphological characters: 1) The use of external seed microsculpturing is valuable in delimiting *S. suksdorfii*, *S. grayi*, and *S. sar-gentii* (see Crow 1979, Prentice 1979, Wofford 1981). The prominent papillae on seeds of *S. sargentii* are diagnostic. 2) Seed length in *S. grayi* is 1.8–3.0 mm, not 1.5 mm as reported by Hitchcock and Maguire (1947). 3) The presence of purple-septate trichomes is valuable in delimiting *S. suksdorfii*. Purple-septate trichomes are not known in *S. grayi* and are rare in *S. sargentii*. The occasional occurrence of these trichomes in S. sargentii does not diminish the importance of this trait in circumscribing S. suskdorfii. 4) Calyx veins are primarily anastomosing in S. suksdorfii and S. sargentii and are nonanastomosing in S. grayi. 5) Petal blades in flowers of S. suksdorfii typically are bilobed and lack lateral teeth; those in S. sargentii usually possess small lateral teeth, and lateral lobes commonly are prominent in S. grayi.

Chemotaxonomy and pollination. The presence of iso-orientin in S. grayi floral extracts and its absence in those of S. suksdorfii provides additional evidence to support the present taxonomic and distributional circumscriptions of these species. Because flavonoids may function in UV absorption as nectar guides, differences in floral chemistry may result from adaptations to different pollinators (Thompson et al. 1972, Harborne 1975). In higher plants, differences in floral morphology that attract different types of pollinators to different species or reduce the possibility of cross pollination between two species are effective prezygotic isolating mechanisms (Stebbins 1977). If floral structure is similar, then diurnal or vespertine flowering also may serve as an isolating mechanism. Silene suksdorfii is a diurnal species, whereas S. grayi is vespertine. Sphyngid moths (after sunset) and syrphid flies (at dawn) were observed visiting S. grayi. No pollinators have been observed on S. suksdorfii.

Ecology. Detailed ecological information is not widely available for S. suksdorfii, S. gravi, or S. sargentii, Excerpts from phytosociological studies (Whittaker 1960, Pemble 1970, Hamann 1972, Taylor 1976, Burke 1982), herbarium collections, regional floras (Ireland 1968, Hunter and Johnson 1983), and field observations, however, provide insight into the types of habitats in which they occur. Silene suksdorfii and S. sargentii are found typically on welldrained substrates in similar habitats in the alpine: in soil pockets on talus slopes, in soil around boulders, and on open, windswept ridges and plateaus. Density and duration of snowpack is variable in areas in which S. suksdorfii is found. Populations on vertical cliff faces, such as those on Red Butte and Broken Top, are subject to winter desiccation and exposure to extreme cold. The ability of S. suksdorfii to grow on cliff faces may depend on the snowmelt water from snowbeds in crevices of rocks and on the ability of poikilohydric mosses to rapidly absorb snowmelt and rainfall, as well as to trap soil (Billings and Mooney 1968, Grime 1979, Walter 1979; D. W. Showers, pers. comm.). Areas in which S. sargentii occurs often are not free of snow until midsummer and dry out rapidly following snowmelt. Populations of S. gravi occur largely on welldrained substrates, but several alpine populations occur in moist, poorly-drained soils located commonly in glacial basins (e.g., Mount Shasta), or on slopes below snowfields. For example, Ferlatte (1974)

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reported a population of *S. grayi* growing on a granitic slope below a permanent snowfield on Thompson Peak in the Trinity Alps. The presence of other moisture-tolerant taxa at this site is indicative of the poorly-drained nature of the soil.

Certain populations of *S. suksdorfii*, *S. grayi*, and *S. sargentii* occur in alpine habitats below climatic timberline. These populations occur in areas where localized climatic and edaphic conditions result in the formation of alpine-like microhabitats at elevations lower than typical of alpine habitats (Daubenmire 1954, Tranquillini 1979, Walter 1979). The existence of azonal alpine is significant in understanding the distribution of *S. suksdorfii* in California because climatic timberline in northern California occurs at 2800 m. The presence of suitable azonal alpine environments at Lassen Volcanic National Park and on Mount Shasta explains the occurrence of *S. suksdorfii* and other species typical of the alpine below that elevation.

KEY TO SPECIES

Blades of petals 2-lobed or with 4 unequal lobes.

Calyx 10-14 mm long; blades of petals 2.5-3.5 mm long; basal lvs. 1-2 mm broad; seeds ca. 1.5 mm long.

Calyx trichomes hyaline-septate (rarely purple-septate); seeds with tessellate faces and marginal papillae (visible with hand lens). Plumas to Inyo cos., CA; NV . S. sargentii
Calyx trichomes purple-septate; seeds tessellate, without marginal papillae. Volcanic peaks, Shasta and Siskiyou cos., CA; n.S. suksdorfii

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ANNOUNCEMENT

MARY DEDECKER SYMPOSIUM

Co-sponsored by the University of California White Mountain Research Station The California Native Plant Society The Bristlecone Chapter of the CNPS 30 April, 1–3 May 1987 Bishop, California

The University of California White Mountain Research Station with the California Native Plant Society and its Bristlecone Chapter are cosponsoring a symposium and field trip honoring Mary DeDecker. The topic of the symposium is the flora and plant biology of the eastern Sierra, Owens Valley, White-Inyo Mountains and western Basin and Range Provinces. Palynology and legislation related to preservation of plants in eastern California and western Nevada also are included as symposium topics.

A field trip will be lead by Mary DeDecker, a member of the BLM staff, and others to the Eureka Dunes on Saturday, 2 May. A cookout-BBQ will be held in the Eureka Dunes following the field trip.

For additional information contact Dr. Clarence A. Hall, Jr., White Mountain Research Station, 6713 Geology Building, University of California, Los Angeles, CA 90024; phone: (213) 825-2093.